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**Transitional fossils illuminate early evolution of the ant-like stone beetle tribe Leptomastacini
(Coleoptera: Staphylinidae: Scydmaeninae)**

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Running title: Transitional Scydmaeninae in Burmese amber

The ant-like stone beetle supertribe Mastigitae (Staphylinidae: Scydmaeninae) comprises nine extant and five extinct genera that exhibit unusual morphological specializations and ecological adaptations. Recent discoveries of mastigite fossils from the middle Eocene to Upper Cretaceous deposits have significantly improved our knowledge of the evolutionary history of this group, yet a direct fossil record for two modern tribes of unclear affinities, *i.e.*, Leptomastacini and Papusini, is lacking. Herein we describe a new genus and species, †*Archemastax divida* **gen. et sp. nov.**, based on two well-preserved individuals entombed in mid-Cretaceous Burmese amber (*c.* 99 Ma), representing the earliest known representative of Leptomastacini. †*Archemastax* possesses both plesiomorphic features and derived characters, with a few important traits shared with extant members of Papusini and Clidicini. A dataset of 70 morphological characters scored for 29 species of Mastigitae was analyzed using maximum parsimony and Bayesian inference; both analyses recovered a sister relationship between †*Archemastax* and extant leptomastacines. However, in the former analysis Leptomastacini was recovered as sister to the remaining Mastigitae, while the latter indicated an origin of Leptomastacini from within Clidicini. Although a close affinity between †*Archemastax* and Papusini was not supported by our analyses, similarities in some shared characters of these two groups are discussed.

Keywords: evolution, transitional form; Mastigitae; Burmite; mid-Cretaceous

Introduction

The supertribe Mastigitae of the subfamily Scydmaeninae constitutes a small group of ant-like stone beetles, represented by some 100 species classified in nine extant and five extinct genera (Jałoszyński 2016a; Jałoszyński *et al.* 2018). The members of this group have received extensive attention from modern taxonomists and systematists because of their unusual morphological specializations and ecological adaptations, as well as highly disjunctive distributions. Some African members are known to occur in dense populations, actively patrolling and copulating in open habitats by day (Jałoszyński *et al.* 2015), while others in North America inhabit a desert environment, and are active during the nights in the hottest season of the year (O’Keefe 2003). One group (Mastigini) occurs disjunctively in the Mediterranean region and South Africa (Leleup 1968; Bordoni & Castellini 1973), raising questions on what factors may have shaped their current distribution.

Five tribes were recently proposed after a comprehensive morphology-based phylogenetic analysis (Jałoszyński *et al.* 2018), which was followed shortly by a morphological revision of all genera (Jałoszyński 2018). These studies provided much clarity on some otherwise previously poorly known groups, and offering a sound base for future descriptions of new taxa in a phylogenetic context. The evolutionary history of Mastigitae has evidently become a subject of major interest following continuing discoveries of a largely number of extinct taxa from the mid-Cretaceous Burmese to middle to upper Eocene Baltic and Rovno ambers (Cai & Huang 2016; Jałoszyński 2012, 2016b; Jałoszyński *et al.* 2017; Jałoszyński & Perkovsky 2016; Yin *et al.* 2017a, 2017b, 2018a). From these discoveries, we are able to safely conclude that some of the modern tribes, such as Mastigini and Clidicini, had an ancient origin dating back at least to the lowermost Cenomanian (*ca.* 99 Ma), when many morphological specializations of these groups were already evidently analogous, if not homologous, to those of their modern relatives.

Among all mastigitae tribes, two are of particular interest with regard to their unusual morphology and elusive phylogenetic positions. The tribe Leptomastacini is represented by 30 species and subspecies grouped in three extant genera, inhabiting mostly cryptic environments (*e.g.*, subterranean) in the Western Palearctic region. Morphological characters reflecting their peculiar lifestyle include the flattened habitus, and strongly reduced or absent compound eyes and functional wings. In *Leptomastax* Pirazzoli, the head appears to be strongly transverse, with extremely elongate, falciform mandibles lacking subapical teeth, but with dense oblique rugae on the cutting edge (Castellini 1996). This was suggested to be associated with their specialized predatory behavior in narrow spaces between soil particles (Jałoszyński 2018). The other tribe, Papusini, stands as one of the most enigmatic groups within Mastigitae. A single genus and nine species inhabiting desert environments occur in southwestern United States and northwestern Mexico. Members were observed to run on sand during the night and were collected under small volcanic rocks during the day, suggesting a nocturnal lifestyle (O’Keefe 2003). The most distinct morphological specialization of this group is their large eyes which are diagnostic for this group, but it remains untested whether this trait is correlated with their unusual habits.

Although the monophyly of Leptomastacini was strongly supported in all previous phylogenetic analyses, the inter-tribal relationships among the Mastigitae are inadequately resolved, with deeper nodes frequently receiving low statistical support (Jałoszyński *et al.* 2018). This is probably due to the fragmentary knowledge of extant diversity resulting in an inadequate sampling of taxa, as well as the inclusion of the many fossil taxa that lacking a vast majority of morphological information. The

placement of Papusini is particularly unstable, given that the mosaic of character occurring in this group are shared with different tribes (Jałoszyński 2018), and whether these characters are homologous or not remains an open question. Herein we describe a new extinct genus and species probably belonging to the stem lineage of Leptomastacini, from the upper Albian to lower Cenomanian Burmese amber. The new taxon exhibits both plesiomorphic features and derived characters, and with some of them shared with Papusini and Clidicini. Our discovery of such a transitional form adds an important piece towards our understanding of the palaeodiversity and morphological disparity of the Mastigitae, especially since it may be of particular importance for understanding the early evolution of the Leptomastacini.

Material

The holotype (NIGP168713) is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (NIGP); the paratype (SNUC-Paleo-0044) is housed in the Insect Collection of Shanghai Normal University, Shanghai, China (SNUC). The fossil specimens described here were obtained from amber deposits in the Hukawng Valley of Kachin, northern Myanmar (26°21'33.41"N, 96°43'11.88"E; Cruickshank & Ko 2003; Grimaldi & Ross 2017). Maps showing the amber-yielding locality and the amber forest 99 mya were provided in Kania *et al.* (2015) and Yin *et al.* (2018b). The age of Burmese amber, once widely regarded as of Eocene age (Chhibber 1934), has been recently established as the earliest Cenomanian (98.79 ± 0.62 Ma) based on U-Pb dating of zircons (Shi *et al.* 2012), which agrees with a general age predicted by Grimaldi *et al.* (2002) based on key bioinclusions. Nevertheless, other workers have suggested slightly older ages, either within the late Albian (Cruickshank & Ko 2003; Ross *et al.* 2010) or near the Albian-Cenomanian boundary (Rasnitsyn *et al.* 2016; Mao *et al.* 2018).

Two extant species of Leptomastacini were examined for morphological comparisons. The material is deposited in SNUC. Their label data are quoted verbatim here, with different labels separated by a slash:

Leptomastax stussineri Reitter, 1880: 1 ex., 'CROATIA: Istra, Limski kanal, 20 m, 13.iv.2009, sifting in forest, P. Hlaváč lgt. / *Leptomastax stussineri* Reitter, P. Hlaváč det., 2009'.

Ablepton treforti Frivaldszky, 1877: 2 exs, 'ROMANIA, Mtii. Mehedinti, Motru Sec., pest. Lazului env., 9-10.5.2015, V. Zieris lgt. / *Ablepton treforti* Frivaldszky, P. Hlaváč det., 2017'.

Methods

The holotype and paratype were cut using a handheld engraving tool and polished using sandpapers of different grits and rare earth polishing powder. Pictures of the fossil were made either using a Canon EOS 5D Mark III digital camera, equipped with a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and an attached Canon MT-24EX twin flash as light source, or using a Zeiss Axio Imager 2 light microscope with an attached digital camera under fluorescence microscopy. Scanning electron micrographs of extant species were produced using a Hitachi SU8010 Field Emission Scanning Electron Microscope. Montage images were produced in Zerene Stacker (version 1.04), and all images were optimized and grouped in Adobe Photoshop CS5 Extended.

Phylogenetic analyses

To test the phylogenetic position of the new fossil taxon within Mastigitae, we incorporated the new material into a previously published dataset (Jałoszyński *et al.* 2018). A total of 70 non-additive and

unordered adult morphological characters were included. These include the 69 characters scored in Jałoszyński *et al.* (2018) and one additional character (69: Modified broadened setae on mouthparts). Characters with a '*' were modified in definition or in coding for a few taxa (File S1). Inapplicable character states are indicated by 'en' dashes (–), and missing data indicated by question marks (?). The data matrix was assembled in WinClada v1.00.08 (Nixon 2002); characters are numbered starting from 0 as required by TNT (File S2).

Parsimony analysis was conducted in TNT v1.5-beta (Goloboff & Catalano 2016) under implied weighting (default weighting function $K = 3$) using the 'Implicit enumeration' strategy; the collapsing rule was switched to 'rule 1'. Standard Bootstrap and Bremer support values were also calculated in TNT. Character mapping on the strict consensus tree was made in WinClada Ver. 1.00.08 (Nixon 2002). The morphological data matrix and the character list and character states are presented in Files S1–2. Bayesian analysis was performed using MrBayes 3.2.6 (Ronquist *et al.* 2012) under the Mk model. The search consisted of two Markov chain Monte Carlo (MCMC) runs of two chains and was terminated at ten million generations. Convergence was determined by the standard deviation of split frequencies having dropped below 0.0075, and further verified by estimated sample sizes higher than 200 in Tracer v1.6 (Rambaut *et al.* 2013), indicating sufficient estimation of the posterior. The first 25% of trees were discarded as burn-in. The consensus tree of both MCMC runs was rooted on *Euaesthetus ruficapillus* (Lacordaire). The Nexus file used for this analysis is available as File S3. All trees were optimized and annotated in FigTree v1.4.3, Adobe Illustrator CS5, and Adobe Photoshop CS5 Extended.

Systematic palaeontology

Family **Staphylinidae** Latreille, 1802
Subfamily **Scydmaeninae** Leach, 1815
Supertribe **Mastigitae** Fleming, 1821
Tribe **Leptomastacini** Casey, 1897

†*Archemastax* **gen. n.**

Type species. †*Archemastax divida* **sp. n.** (here designated)

Generic diagnosis. †*Archemastax* can be separated from all extant leptomastacine genera by the following combination of characters: 1) head dorsum, mouthparts, and antennae with modified, thickened setae, 2) maxillary palpomeres III–IV clearly demarcated, not forming a compact oval club, 3) distal margin of palpomere III and basal margin of IV straight and truncate, non-oblique, 4) palpomere IV slightly longer than wide, 5) elytra with regular longitudinal rows of large punctures, 6) metathoracic wings fully developed, 7) anterior margin of prosternite, and meso- and metaventrite lacking leaf-like broadened setae, 8) metaventrite with distinct median longitudinal carina, and 9) mesocoxa with row of elongate thickened bristles.

Description. Body (Figs 2, 5A–B) small, length slightly over 1.5 mm, reddish-brown, flattened, dorsally finely setose; modified setae distributed mostly on antennae and head, either elongately spatulate or short to very long and thickened, distributed mostly on antennae and head.

Head capsule (Figs 1, 2C, 5B; *h*) divided into large and exposed anterior part and much smaller, rounded and flattened 'neck' region retracted into prothorax and demarcated by distinct occipital

constriction; 'neck' region about as broad as half width of head. Anterior part of head flattened and slightly broader than long, roundly triangular in shape, with rounded sides of vertex, narrower than pronotum and broadest near posterior margin. Compound eyes (Fig. 5D; *ce*) dorsolateral, oval, large, located at posterior half of head, roundly projecting laterally, each eye composed of about 30 small facets (ommatidia). Vertex (Fig. 3B; *ve*) strongly transverse and weakly, evenly convex, with posterior margin straight or nearly straight at middle and pair of long, thickened posterolateral setae (Figs 3B, 5D). Tempora long and rounded. Frons (Fig. 3B; *fr*) between antennal insertions subtriangular, anteriorly demarcated by deep and narrow frontoclypeal groove. Clypeus (Fig. 3B; *cl*) short and broad, with rounded sides appearing to slightly project behind external margin of each mandibular base, with one elongate, thickened seta on each side. Antennal insertions located dorsally in sub-median area of head. Gular plate (Fig. 3C; *gp*) lacking sutures.

Antennae (Figs 3A, 5A; *ant*) much shorter than body; scape (Fig. 3A–B; *al*) about 2.5 times as long as broad; pedicel (Fig. 3A; *a2*) distinctly longer than antennomere III and evenly broadening from narrow base to apex; antennomeres III–IV (Fig. 3A; *a3–4*) slightly elongate, V–X (Fig. 3A; *a5–10*) mostly transverse and weakly thickening distally, each with narrow and short basal stalk; antennomere XI (Fig. 3A; *a11*) elongate and slightly asymmetrical. Antennomeres covered with dense and evenly distributed short and thin setae (Fig. 3A; indicated by blue arrow) and much longer, strongly flattened and broadened spatulate setae around distal margin of each antennomere except XI (Fig. 3A; indicated by red arrow).

Labrum (Fig. 3B; *la*) strongly transverse, with broadly concave anterior margin; dorsal surface with two long and thickened setae at each side. Mandibles (Fig. 3B–C; *ma*) symmetrical, each subtriangular but relatively slender, with broad base and long, curved and moderately sharp apical tooth, with one elongate thickened seta on ventral surface. Maxilla (Fig. 30) with large but relatively short cardo; stipes elongate, with one elongate thickened seta, demarcated from lacinia and galea, which bear dense row of distally thickened setae; palpifer broad and elongate, with one elongate thickened seta at apicolateral margin; maxillary palpus composed of minute palpomere I, elongate and distally broadened palpomeres II–III (Figs. 3C; *mp2–3*), and short and conical palpomere IV (Figs. 3C; *mp4*); base of palpomere IV clearly narrower than base of palpomere III; all palpomeres finely setose, only apex of III with longer and thicker lanceolate setae around apex. Labium (Fig. 3C) with broad submentum (Fig. 3C; *smn*) posteriorly not demarcated from gular region, bearing pair of long and thickened setae near its anterior margin; mentum (Fig. 3C; *mn*) sub-trapezoidal and strongly transverse, with anterior margin slightly concave; prementum (Fig. 3C; *pmn*) sub-trapezoidal, broadest distally, lacking demarcated ligula, with broadly separated bases of labial palpi; labial palpus (Fig. 5C; *lp*) composed of three palpomeres: palpomere I small, elongated, palpomere II large, strongly elongated and slightly broadening distad, palpomere III narrow and pointed, about as long as II; palpomere I has one and palpomere II has two modified thickened setae (Figs. 3C, 5C) near apex.

Prothorax flattened and elongate, broadest near anterior 2/5. Pronotum (Figs. 1A, 1C, 5B; *p*) with all margins rounded or sides in posterior half nearly straight; anterior corners broadly rounded, posterior corners indistinct, obtuse-angled; pronotal base apparently lacking pits, impressions, grooves or carinae. Prosternum (Fig. 3C) with basisternal part more than twice as long as coxal part, laterally completely fused with hypomera, notosternal sutures not visible in both specimens. Coxal region demarcated anteriorly by carina extending laterally up to apices of subtriangular adcoxal hypomeral lobes projecting mesally. Procoxal cavities broadly open. Ventral surface of prothorax largely asetose and glabrous; lacking leaf-like setae.

Mesoventrite (Fig. 4C) sub-trapezoidal, broadening posteriorly, lacking strongly flattened, leaf-like setae. Mesoventral intercoxal process long, narrow and weakly convex but distinctly carinate (Fig. 4C; *msc*) at middle, fully separating mesocoxae, weakly but distinctly narrowing posteriorly and fused with metaventrite. Metanotum with fully developed hind wings (Fig. 5A–B; *hw*). Metaventrite (Fig. 4B–C) short, sub-quadrate, with lateral margins rounded; mesocoxal cavities with marginal carina encompassing each cavity nearly entirely; posterior margin with broad metaventral intercoxal carina (Fig. 4B–C; *mtc*), lacking foveae and leaf-like setae.

Elytra (Figs 4A, 5B; *e*) oval, flattened, humeral calli and basal impressions indistinct or lacking, with rounded apices; elytral disc with distinct large and deep punctures arranged in nearly complete longitudinal rows.

Legs moderately long, slender. Pro- and mesocoxa elongately subconical, metacoxa with nearly hemispherical basal part and subconical distal part. Mesocoxa with three to four long and thickened coxal bristles (Fig. 4C; indicated by black arrow). All trochanters short and subtriangular. Femora weakly clavate. Tibiae robust, all nearly straight. Tarsi short but slender, sub-cylindrical, tarsomeres decreasing in length but not in width from I to IV, tarsomere V strongly elongate. Claws of all tarsi curved, directed and divergent distally; empodium with pair of short, thickened setae (Fig. 2A; indicated by red arrows).

Abdomen (Figs 4B, 5A; *s3–8*) with sternite III not fused with metaventrite, about as long as sternites IV and V together, sternites VI–VII each about as long as V, sternite VIII 1.5 times as long as VII, with rounded posterior margin; sternite III lacking leaf-shaped setae at base.

Etymology. The generic name is a combination of Greek ‘*arkhē*’ (beginning, origin), and ‘*mástax*’ (mouth, jaws). The gender of the new genus is feminine.

†*Archemastax divida* sp. n.

Type material. Holotype: NIGP168713, sex undetermined; upper Albian to lower Cenomanian, Hukawng Valley, northern Myanmar; deposited in NIGP. Paratype, SNUC-Paleo-0044, sex undetermined, same locality and horizon as the holotype; deposited in SNUC.

Diagnosis. As for the genus (*vide supra*).

Description. [Note: measurements are provided only for the holotype, which is in an upright position, while the length of the elytra of the paratype is same as of the holotype.] Body length 1.64 mm. Body elongate, flattened, and uniformly reddish-brown, appendages slightly lighter in color. Head slightly broader than long, broadest at eyes and flattened; length from clypeal anterior margin toward base 0.25 mm, width of head across eyes 0.27 mm; vertex strongly transverse and flattened, indistinctly impressed medially and anteriorly confluent with strongly transverse frons; tempora about as long as eyes in dorsal view, strongly rounded and convergent towards distinct occipital constriction; frons sub-triangular, broad and flattened, descending towards clypeus, with complete and distinct frontal-clypeal groove; eyes large and strongly convex, nearly circular, finely faceted; supraantennal tubercles moderately developed; antennal insertions located anterior to eyes; sculpture of head dorsum not clearly visible; vestiture composed of short, sparse, curved and suberect setae, vertex with one long, thickened setae on each side. Maxillary palpus slightly shorter than head; palpomere I minute and sub-quadrate; palpomere II elongate, length 0.16 mm, evenly broadening from base toward apex; palpomere III elongate, shorter than II, length 0.11 mm, pedunculate at base, strongly broadened distally, truncate at apex, and with ring of thickened lanceolate setae; palpomere

IV short and conical, length 0.04 mm, narrower than III and broadest at base, apical palpal cone present; all palpomeres covered with fine, suberect setae pointed mostly apically. Antennae distinctly shorter than body length, antennal length 0.96 mm, all antennomeres covered with thin, suberect setae, and with modified flattened spatulate setae around apex except for antennomere XI. Pronotum distinctly longer than broad, broadest near anterior 2/5 and strongly narrowing towards base, length of pronotum along midline 0.41 mm, maximum width 0.32 mm, pronotal index (length/width) 1.28; anterior and lateral margins strongly rounded, posterior margin virtually straight, sides in posterior 3/5 evenly constricted; posterior collar short. Punctuation of pronotal disc not visible; vestiture dense, short and strongly suberect. Prothoracic hypomera not delimited; prosternum elongate, without discernible details; prosternum densely covered with very thin, short and suberect setae. Elytra more convex than pronotum, broadest at posterior third; length of elytra along suture 0.98 mm, maximum width 0.50 mm, elytral index (length/width 1.95); each elytron with indistinct or absent humerus, five rows of longitudinal, deeply punctate striae, and nearly rounded apex; vestiture similar to that on pronotum, but setae slightly longer. Metathoracic wings fully developed. Mesoscutellum not observable in both specimens. Mesoventrite short, with narrow mesoventral carina separating mesocoxae. Metaventricle large, much broader than long, sides of ventrite convex, posteromedian part slightly impressed, with complete median longitudinal carina. Abdomen much longer than metaventricle, six abdominal sternites visible, first visible sternite (III) longest; sternite VIII not modified, vestiture finely setose. Pygidium exposed, densely setose. Legs long and slender, tibiae with two apical spines.

Etymology. The specific epithet '*divida*' means 'divided, separated', referring to the transitional morphology of the new species.

Phylogenetic placement of *Archemastax*

Parsimonious analysis using TNT v. 1.5-beta based on a data matrix derived from a modified, previously published dataset (File S1–2) under implied weight analysis ($K = 3$) resulted in 10 most parsimonious trees. A strict consensus tree (with tree length = 150, consistency index = 48, and retention index = 79) was calculated, in which †*Archemastax* was recovered as the sister group of modern leptomastacines (Fig. 6). The monophyly of Leptomastacini was supported by two unequivocal synapomorphies: modified, broadened and flattened setae on thorax and antennae present (character 0, state 1), and modified broadened setae on mouthparts present (character 69, state 1). The topology of our strict consensus cladogram (Fig. 6) is largely similar to that of Jałoszyński *et al.* (2018: fig. 4); note that in both these trees only a clade composed of extant leptomastacines retained a high statistic support. In order to provide a comparison with the result of Jałoszyński *et al.* (2018, fig. S1), we also performed a separate analysis using Bayesian inference; the result again supported the monophyly of †*Archemastax* + extant Leptomastacini (Supplemental Fig. 5; posterior probability = 1). But alternatively, the clade was recovered as being derived from within the Clidicini.

Discussion

Among the three extant (Scydmaenitae, Mastigitae, Cephenniitae) and one extinct (Hapsomelitae) supertribes of the subfamily Scydmaeninae, †*Archemastax* can be assigned to Mastigitae based on

the ant-like general habitus (*i.e.*, with distinct constrictions between head and pronotum and between pronotum and elytra), the antennomere I (scape) being elongate, and much longer than antennomere II (pedicel), the antennae being distinctly geniculate between scape and pedicel, so that the pedicel and flagellomeres are able to bend ventrally, the maxillary palpi being longer than the head, with palpomere IV not dome-like, and the compound eyes located in the anterior part of the head. Six tribes of Mastigitae have been established after a recent phylogenetic analysis comprising all extant and fossil representatives (*sensu* Jałoszyński *et al.* 2018). †*Archemastax* exhibits a mosaic of character states, some of which are shared with the tribe Leptomastacini and others with the tribe Papusini and Clidicini. †*Archemastax* has two elongate, thickened setae on the basolateral portion of the vertex, one pair of similar setae on the anterolateral margin of the clypeus, and two pairs on the anterior margin of the labrum (Fig. 3B). Similarly modified thick or robust setae are also present on the submentum, prementum, maxilla, and labial palpi (Fig. 3C). These structures are not found among modern mastigites except for Leptomastacini (Supplemental Figs 2A–D, 4A–C) comprising three extant genera (*Ablepton* Frivaldszky, *Leptomastax* Pirazzoli, and *Taurablepton* Franz) (Jałoszyński 2018). †*Archemastax* also exhibits strongly flattened broadened spatulate setae around the apices of the antennomeres I–IX (Figs 2A, 5), which are diagnostic for the extant Leptomastacini (Supplemental Figs 2E–F, 4D). These characters provide direct evidences for a close affinity between †*Archemastax* and modern leptomastacines, which is congruent with the result of our phylogenetic analyses (Fig. 6, Supplemental Fig. 5). Exhibiting a number of derived traits, *Archemastax* could be a member of a lineage that diverged prior to the most common ancestor of extant Leptomastacini and subsequently went extinct (a stem group of Leptomastacini), or alternatively, represents the true ancestor that gave direct rise to all living leptomastacines.

Otherwise, †*Archemastax* appears to embody a set of plesiomorphic features that are absent in extant Leptomastacini: 1) maxillary palpomeres III and IV distinctly demarcated (Fig. 3B–C), with apex of palpomere III narrower than base of palpomere IV, and the suture separating III and IV straight and transverse; 2) palpomere IV triangular, slightly longer than broad; 3) compound eyes (Figs 2, 3B–C, 5) large, protruding laterally; 4) elytra bearing large and deep punctures arranged in regular longitudinal rows; and 5) foveae absent (Fig. 2B–C) on the prosternum and pterothorax. In contrast, extant members of Leptomastacini have the maxillary palpomeres III–IV forming a compact oval club, with the suture between palpomeres III and IV strongly oblique (Supplemental Fig 1B); the palpomere IV is much broader than long (Fig. 1, Supplemental Fig. 1B); the compound eyes are strongly reduced or absent (Fig. 1, Supplemental Figs 1A, 2A, 3A); the elytra have only shallow or no punctures (Fig. 1); and the prosternum and pterothorax have large foveae containing leaf-like setae (Supplemental Figs 3B–D, 4E–F). It should be noted that the large eyes of †*Archemastax* are shared with the tribe Papusini, which is diagnostic for the latter group.

The enigmatic Papusini currently contains a single genus (*Papusus*) and nine species distributed in the Nearctic region, inhabiting the driest deserts of North America (O'Keefe 2003). The relationship of Papusini within Mastigitae remains controversial, and its position is particularly unstable (Jałoszyński 2012, 2016b). The most recent analysis (Jałoszyński *et al.* 2018) placed it, albeit with low statistical support, as sister to Leptochromini + (Baltostigini + Mastigini). A similar topology is obtained by the present analysis (Fig. 6). Among the many recent studies on the phylogeny of Mastigitae, a potential affinity of Papusini with Leptomastacini has been reported only once (Jałoszyński 2016b), supported by the presence of mesocoxal lateroventral bristles which are unique for these two groups. Moreover, †*Archemastax* also possesses similarly large compound eyes

that are diagnostic for Papusini, as well as an identical shape of the maxillary palpi. Based on these similarities, it is possible that modern Papusini may be derived from an *Archemastax*-like ancestor (with large eyes) that originated in Laurasia, and later branched off in Laurentia or dispersed into Laurentia from the Eurasian part of Laurasia, to form their current distribution. Nevertheless, it is still uncertain whether the large eyes of Papusini represent a plesiomorphic trait, or a secondarily derived state retained from a different small-eyed group; given that the extant papusines are active during the night (O'Keefe 2003), it is not impossible that the large eyes are a convergently derived trait adaptive to their nocturnal habits.

On the other hand, in a separate Bayesian analysis (Supplemental Fig. 5) the Leptochromini (pp = 1) is comprised in a polytomy (pp = 0.55) within the tribe Clidicini (pp = 0.83), a result substantially different from a similar analysis of Jałoszyński (2018: fig. S1; relationship of Leptochromini within Mastigitae unsolved). The differences between these two analyses may stem from the extensive amount of recoding of several fossil taxa of Clidicini (taxa listed in File S1), as well as a few morphological similarities shared by †*Archemastax divida* and a number of extinct *Clidicus* species. Both †*Archemastax* and the two extinct species of *Clidicus* were reported from a same deposit (Burmese amber). These taxa share a similar form of the maxillary palpus (probably plesiomorphic for Mastigitae), the presence of a collar at the base of the pronotum, the large punctures of the elytra that are regularly arranged in longitudinal rows, and the presence of a median longitudinal carina of the metaventrite (carina present in *C. archaicus* (Cai & Huang), absent in *C. burmiticus* (Yin, Cai, Huang *et al.*)); even the rowed setae (although much thinner) of the mesocoxae in the two *Clidicus* species resemble the bristles of the same body parts in †*Archemastax* (Cai & Huang 2016; Yin *et al.* 2017b; note the genus *Cretoleptochromus* was subsequently synonymized with *Clidicus* by Jałoszyński *et al.* 2018). In that regard, the possibility that †*Archemastax* may diverged from a common ancestor of Leptochromini + Clidicini before mid-Cretaceous cannot be totally excluded, regardless the strongly modified setae of the head and antennae are so unique to Leptochromini and lack of most Clidicini synapomorphies (Jałoszyński 2018) in †*Archemastax*.

Our new discovery of †*Archemastax* from Burmese amber, as stated above, shows a transitional morphology mostly shared between Leptomastacini and Papusini, indicating a relatively later divergence time of these two tribes. Based on the highly modified head and antennae, which are mostly likely homologous to those in the extant leptomastacines, †*Archemastax* can be established as a stem group Leptomastacini and the sister group to extant members of the tribe. Currently, the Mastigitae have much richer fossil records than any other scydmaenine lineages, which have already provided critical insights into the early evolution of this group. However, the inter-tribal relationships within the supertribe are still inadequately solved, therefore a fossil-calibrated molecular phylogeny including all mastigite genera would be required in the future.

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Supporting material

Supplemental Figures 1–4. Morphological features of extant *Leptomastax stussineri* and *Ablepton treforti*.

Supplemental Figure 5. Majority-rule consensus tree of Bayesian inference showing phylogenetic placement of †*Archemastax divida*.

Supplemental File 1. List of characters and character states used in the phylogenetic analysis.

Supplemental File 2. Morphological data matrix for the phylogenetic analysis.

Supplemental File 3. MrBayes Nexus file for the Bayesian analysis of morphological data.

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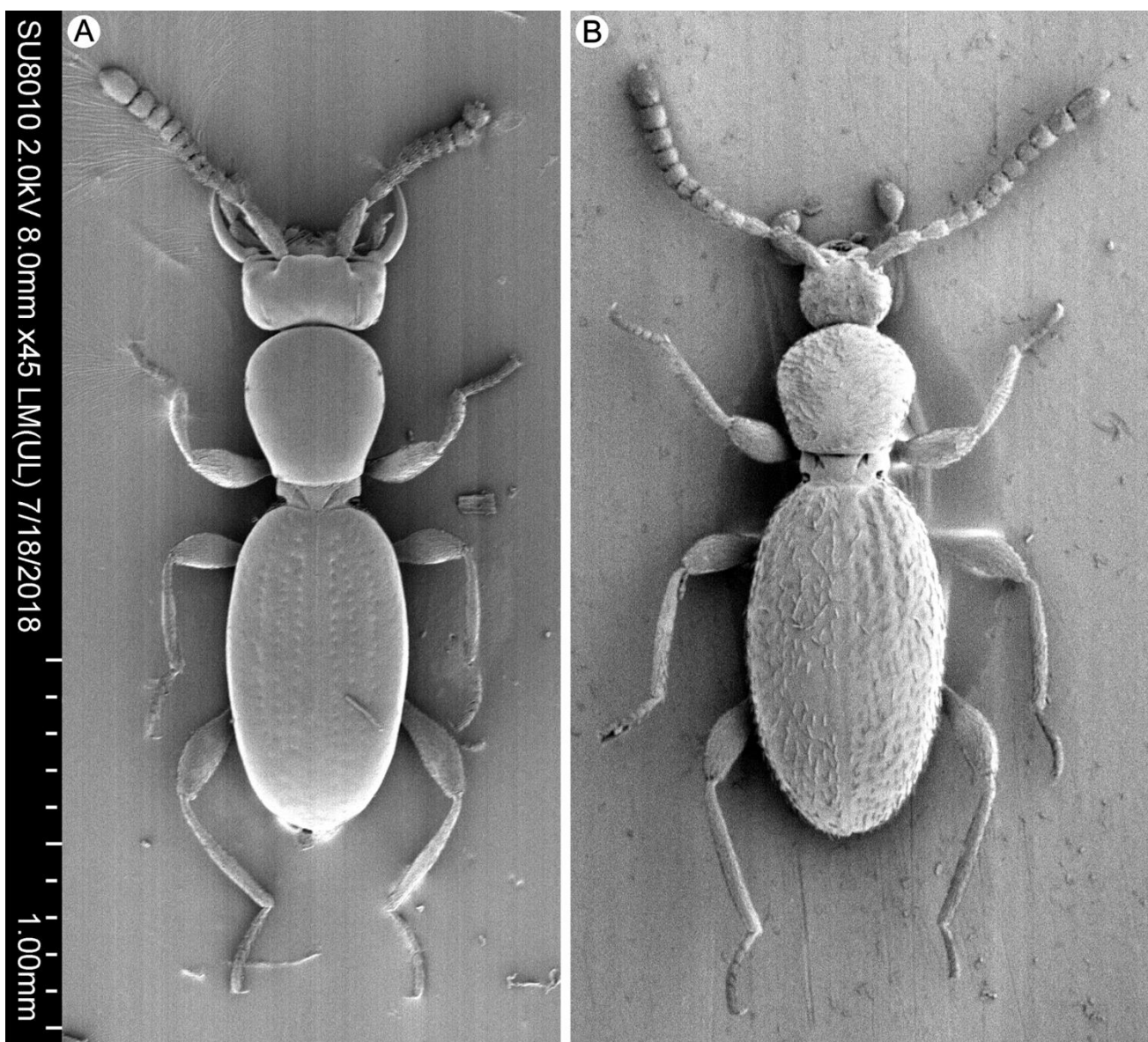


Figure 1

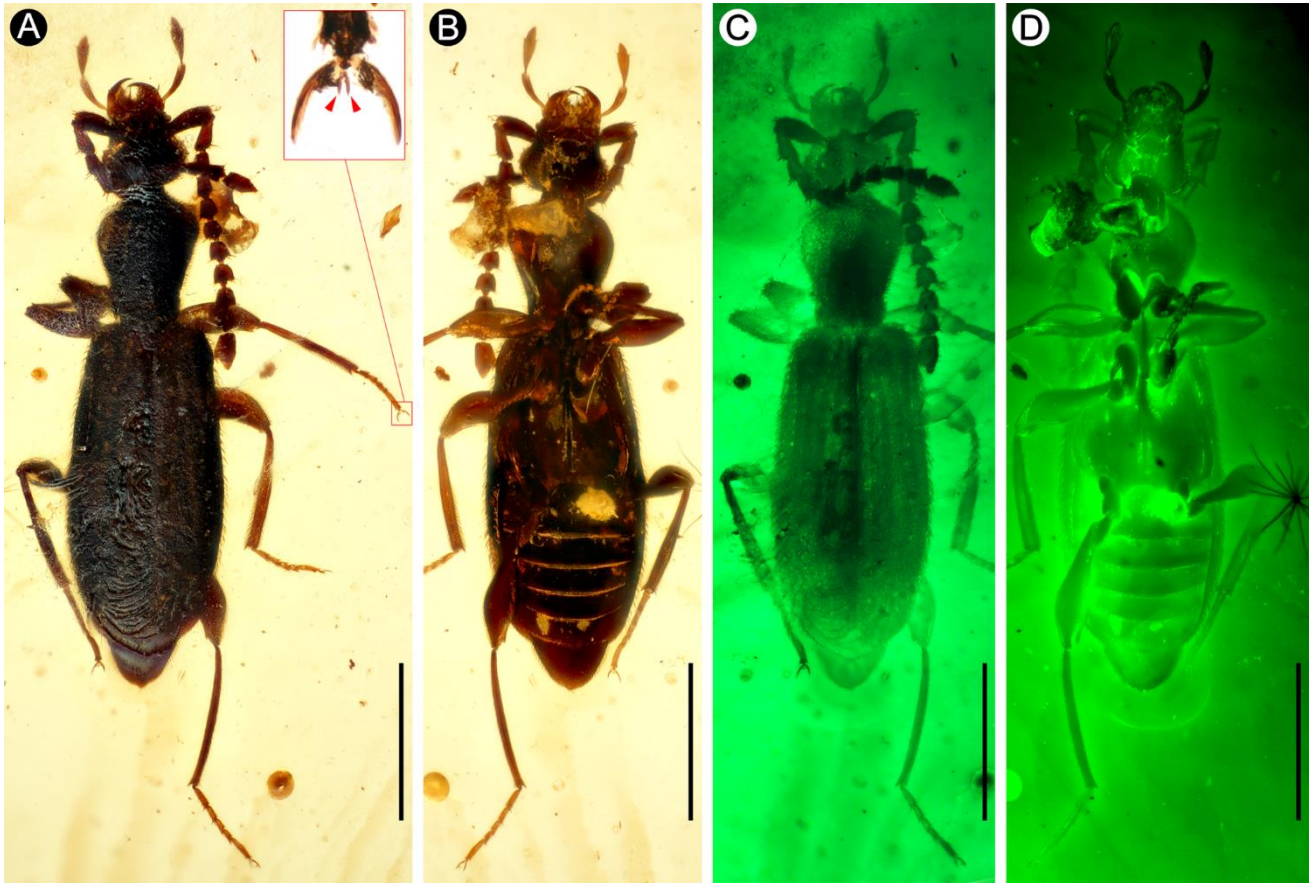


Figure 2

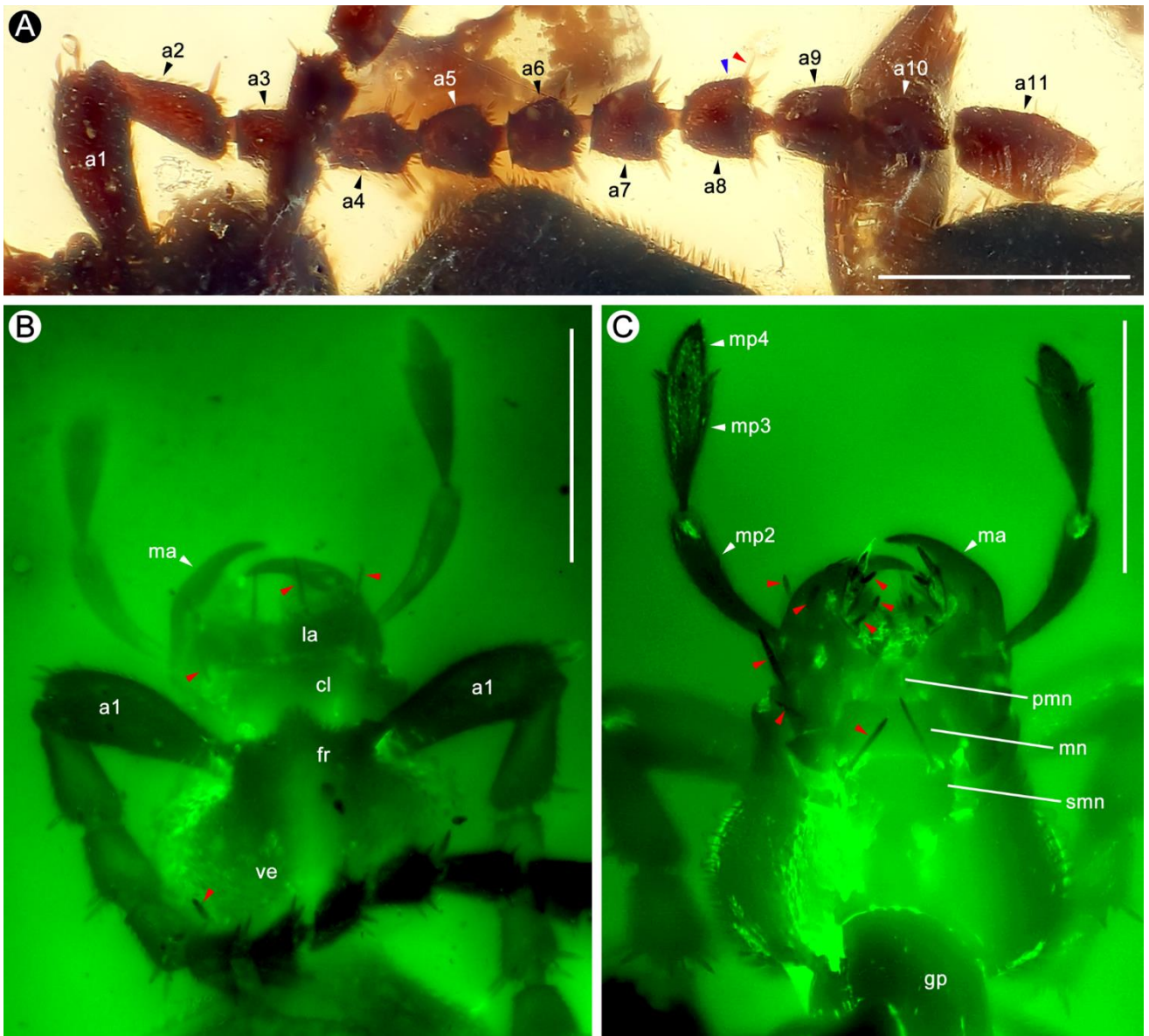


Figure 3

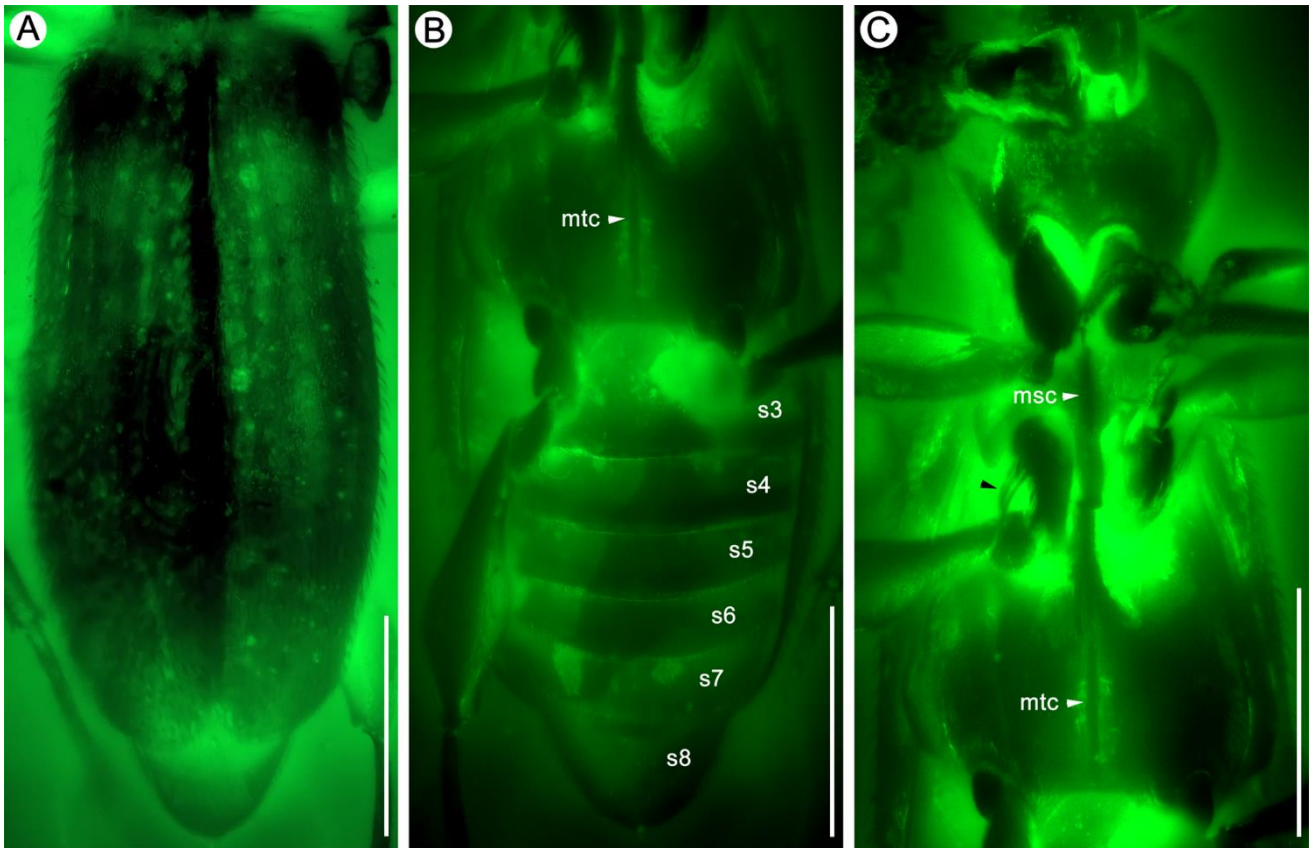


Figure 4

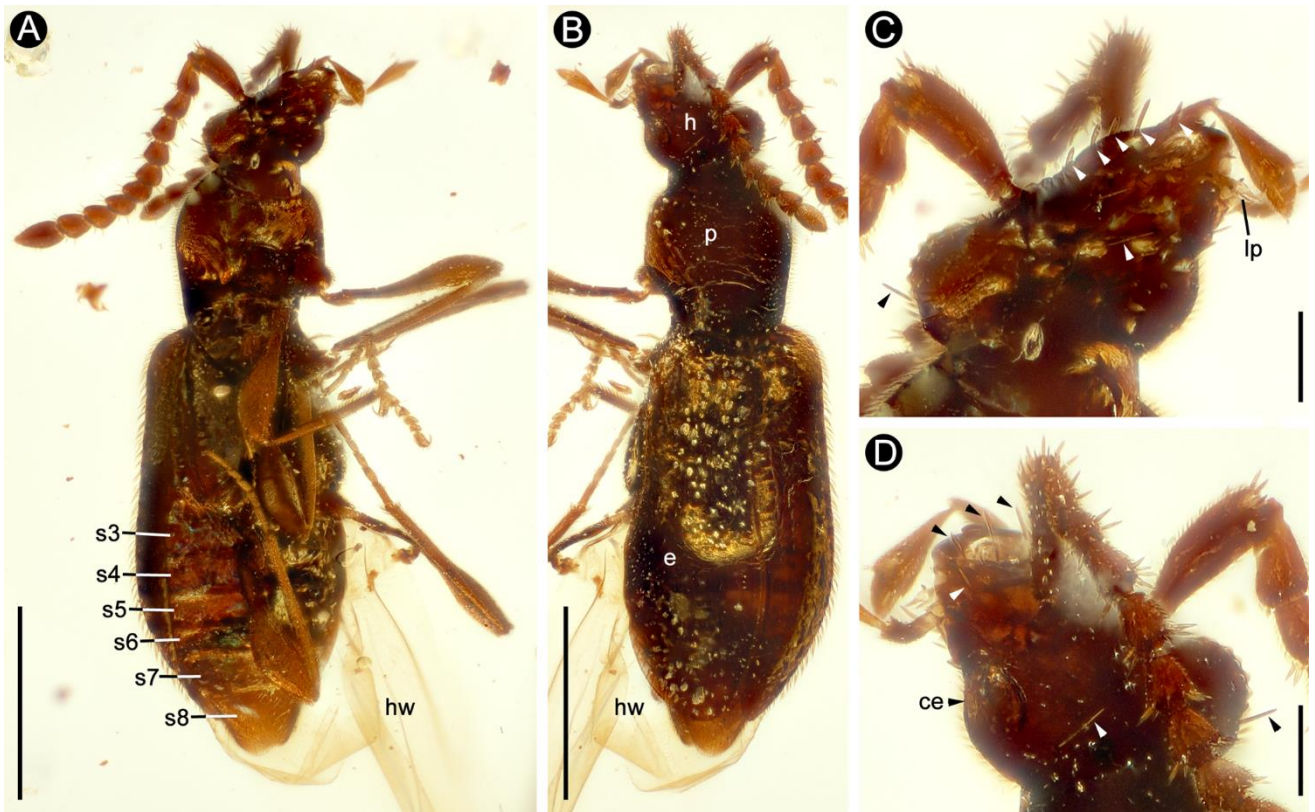


Figure 5

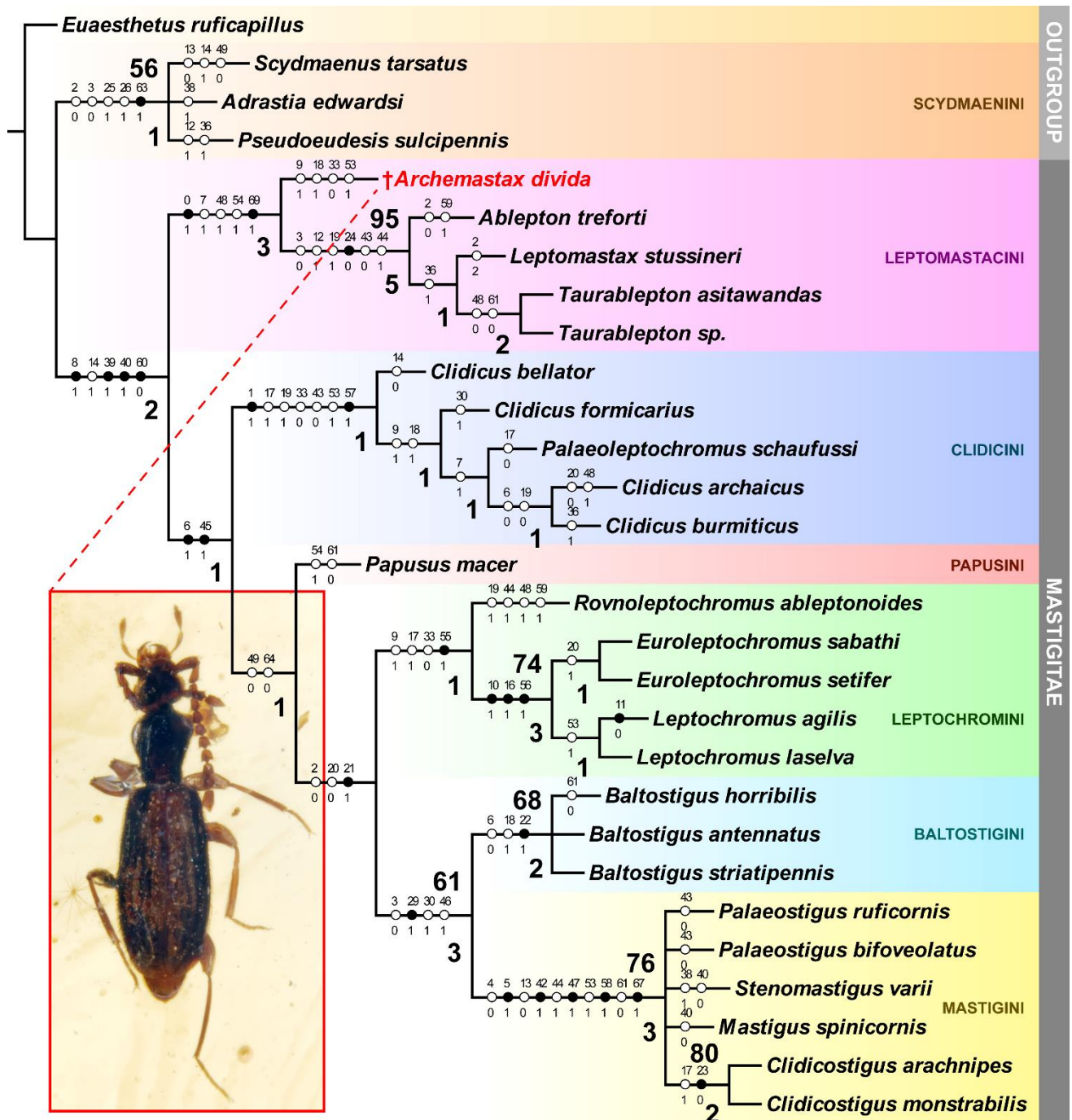


Figure 6

Figure caption

Figure 1. Extant representatives of Leptomastacini. **A**, *Leptomastax stussineri*; **B**, *Ablepton treforti*.

Figure 2. Habitus of †*Archemastax divida*, holotype (NIGP168713). **A–D**, dorsal (A, C) and ventral (B, D) habitus with standard lighting (A, B) and fluorescent lighting (C, D). Scale bar: 0.5 mm.

Figure 3. Morphological details of †*Archemastax divida* **gen. & sp. n.**, holotype (NIGP168713). **A**, antenna; **B–C**, head, in dorsal (B), and ventral (C) view. Blue arrow indicates normal pubescence, and red arrows indicate modified spatulate/thickened setae. Abbreviations: a1–11, antennomeres I–XI; cl, clypeus; fr, frons; gp, gular plate; la, labrum; ma, mandible; mp2–4, maxillary palpomeres II–IV; mn, mentum; pmn, prementum; smn, submentum; ve, vertex. Scale bar: 0.2 mm.

Figure 4. Morphological details of †*Archemastax divida* **gen. & sp. n.**, holotype (NIGP168713). **A**, elytra; **B**, metaventrite and abdomen; **C**, prosternum, and meso- and metaventrite. Arrow indicates row of thickened setae on mesocoxa. Abbreviations: msc, median mesoventral carina; mtc, median metaventral carina; s3–8, sternites III–VIII. Scale bar: 0.3 mm.

Figure 5. †*Archemastax divida* **gen. & sp. n.**, paratype (SNUC-Paleo-0044). **A–B**, ventral (A) and dorsal (B) habitus; **C–D**, head, in ventrolateral (C), and dorsolateral (D) view. Arrows show modified thickened setae. Abbreviations: ant, antenna; ce, compound eye; e, elytra; h, head; hw, hind wing; lp, labial palpus; p, pronotum; s3–8, sternites III–VIII. Scale bar: 0.5 mm in A–B; 0.1 mm in C–D.

Figure 6. Strict consensus cladogram of 10 most parsimonious trees obtained by the ‘Implicit enumeration’ analysis of a data matrix of unweighted and unordered adult morphological characters under implied weighting ($K = 3$; tree length = 150; consistency index = 0.48; retention index = 0.79), showing phylogenetic placement of †*Archemastax divida* **gen. & sp. n.** Standard Bootstrap (≥ 50) and Absolute Bremer support values (≥ 1) are shown above and below branches, respectively. Unambiguously optimized character changes are plotted along internodes. Black circles indicate unique character changes; white circles indicate parallelisms or reversals; character numbers are above circles; character states below circles.